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THE MORPHOLOGY OF *LUFFIA FERCHAULTELLA* (STEPHENS) AND A COMPARISON WITH *LUFFIA LAPIDELLA* (GOEZE) (LEP., PSYCHIDAE).

By Richard S. McDonogh, B.Sc., D.I.C.

Introduction.

The Psychid family Luffiidae contains, according to Tutt, two genera, *Luffia* Tutt and *Bacotia* Tutt. *Luffia* has two species, *L. lapidella* (Goeze) and *L. ferchaultella* (Stephens). *Bacotia* has one species, *B. sepium* Speyer. The family forms an intermediate group between the Micro- and the Macro-Psychids. The characters indicating this position have been outlined by Chapman (1899a) and Tutt (1900). In all species the female is apterous. *Bacotia sepium* is not considered here. It is bisexual and is an arborial form. *L. lapidella* is a bisexual species having larvae which are supposed to feed on rock-lichens, while *L. ferchaultella* is not known to have males but is a parthenogenetic species whose larvae feed on tree-lichens (*Lecanora* spp.). The species of *Luffia* provide two distinct biological problems for solution. First, are the bisexual and the parthenogenetic forms really distinct species or only variations differing in mode of reproduction, such as are known in various Hymenoptera (e.g. *Pelecinus*, *Rhodites*). Second, it has been stated (Chapman, 1899 (b), 1901 (a) and 1901 (b)) that the parthenogenetic form has become split up into a number of local races; the reality of the distinctions between the races is still, however, in doubt. Finally, the general morphology of the species and of the early stages has not yet been very satisfactorily treated.

Investigations upon the occurrence of local races in *L. ferchaultella* are being dealt with elsewhere. This paper consists of a short account of the morphology of the two species of *Luffia*

recognised by Tutt and a discussion of the validity of them being regarded as distinct species.

Acknowledgements.

This investigation has been carried out at the Imperial College of Science and Technology Biological Field Station, Slough, Bucks, under the direction of Professor J. W. Munro, D.Sc. I wish to thank Dr. O. W. Richards for suggesting the work, and for his invaluable assistance and great interest throughout. I also wish to thank H. C. Gough, B.Sc., for sending me larvae of *L. lapidella* and *L. ferchaultella* from the Channel Isles.

General Morphology.

(1) *INTRODUCTION.*

Tutt is almost the only author who has described the external morphology of the Luffiidae. Tutt's descriptions of *L. ferchaultella* and *L. lapidella* suffer from the defect that they are not comparative. Some of his remarks are either inaccurate or misleading. For instance, he states that in *Luffia* larvae the head and thoracic plates are black. Actually they are dark brown. The abdomen is only dark grey in fairly old larvae, from the fourth instar upwards. Previous to the fourth stage the abdomen is a light yellow. In the first instar it is very pale in colour. The presence of the setae on the head is merely noted ; no attempt is made to describe their position. The light marking on the prothorax is described as V-shaped and smoke-coloured in *Luffia ferchaultella,* and as triangular and grey in *L. lapidella*. In fact, this marking is the same in both species. The skeleton of the head of *L. ferchaultella* has the ' polygonal reticulation as of closely fitting cells,' which Tutt describes as being characteristic of *L. lapidella* only. The dorsal anal plates are considerably lighter brown than is the head-colour, yet they are described as ' dark-coloured (but not quite black).'

Tutt did not publish a description of the pupa of the two species of *Luffia* which he recognised, in such a manner that they can be distinguished from one another. The matter contained in the descriptions is fairly accurate apart from one or two small points, notably his identification of some of the sclerites of the head of *L. ferchaultella* pupa. What he calls the labrum, the large size of which he remarks upon, is more likely to be the clypeus. The actual labrum would then be the small triangular structure immediately below the clypeus. What Tutt calls the jaws, and rather uncertainly described as ' carrying (or rather carried by) a basal process,' are the maxillae, the true mandibles being the above ' basal process.' The account of the pupa of *L. lapidella* female is shorter and less useful than the description

of the parthenogenetic female pupa. The male pupae of *L. lapidella* obtained from Guernsey do not agree very closely with Tutt's description, especially in the positions of the ends of the legs.

Tutt's descriptions of the female adults of both species are moderately accurate. They suffer from the same fault as do the pupal descriptions: they are not specific accounts, and it is not possible to distinguish with certainty between the two forms. The absence of figures of all stages of the species has been remedied in the present paper.

No previous work on the Lufliidae dealt with the internal morphology. Although the anatomy of the Lepidoptera is more or less uniform and well-known, it was thought that the parthenogenetic character might be reflected in the arrangements of the reproductive organs, especially in the presence of otherwise of a receptaculum seminis. With reference to this point, von Siebold (1857), describing the moths of the genus *Solenobia* (belonging to the Solenobiidae of Tutt, but to the group Talaeporiae of von Siebold), which are related to the Luffiidae, states that all the females had the bursa copulatrix and receptaculum seminis, but they were empty and unexpanded in the parthenogenetic forms. He said that the ovaries appeared to be exactly like those of virgin females. He studied the species *S. triquetrella* and *S. lichenella*.

(2) *EGG.*

This has been adequately described by Tutt (1900: 249). They are yellowish-white, ovoid, 0·5 mm. × 0·375 mm. They are not *mixed* with hair-scales from the anal-tuft of the female, as Tutt states, but the latter are deposited on the top of the batch of eggs, which is laid in the old pupa case.

(3) *LARVAE.*

The larvae of the bisexual species of *Luffia* have not been studied in much detail owing to lack of material. The few specimens obtained did not appear to differ from those of *L. ferchaultella* except in size and perhaps colour. The body proportions stated by Tutt to differ in the two species are not reliable. The size of the abdomen varies considerably in each instar. The head diameter of comparable instars is one of the few structural characters differentiating the two forms. There also appears to be a higher proportion of the larvae of *L. lapidella* with dark grey coloured abdomens than occur in the smaller species. Whether the early instars of the former species have a lighter coloured abdomen, as suggested by Tutt and also mentioned by Réaumur, cannot be stated here. The larvae of the parthenogenetic moth are often dark grey in the last two instars, but the early stages are always light yellow, becoming darker as they pass through each instar.

The average head diameter of the last instar was 0·92 mm. [standard deviation ±0·03] in the *L. lapidella* larvae and 0·71 mm. [standard deviation ±0·025] in the *L. ferchaultella* larvae.

The positions of the setae on the head capsule of the *Luffia ferchaultella* larvae are shown in figs. 1 and 2 (Plate I). All the larvae examined appeared to have all the setae present at all stages in their life-history.

The four setae on the latero-posterior part of the head are very small and difficult to observe in the small instars. The anterior setae are all large. The seta lateral to the frontal suture is the largest. Besides the setae, the head-capsule has a number of small structures which resemble the bases of setae, but they never bear any. There is a tendency for these structures to be arranged on the head so that one of them and two setae form the apices of a triangle.

A dorsal view of the tentorium of the larva is figured in fig. 4 (Plate I). The tentorial bridge and the hypostomal bridge join the two sides of the head-capsule, the edge of which is strengthened by the invagination of the frons. This support of the head-capsule meets the anterior tentorium at the latero-anterior corner of the clypeus. The anterior tentorium curves posteriorly and ventrally until it joins the tentorial bridge and the posterior tentorium, which is a short stout projection from the posterior corner of the hypostomal region.

The mouth-parts of the larvae are typically lepidopterous. The mandibles have five teeth, the innermost (dorsal) one being very blunt (fig. 3, Plate I). There are two setae situated near the condyle. The spinneret is borne on a strongly sclerotised prementum which is hemispherical and capable of considerable antero-posterior movement (fig. 8, Plate I). The cardo appears to be represented by two sclerites. The medial edge of the stipes is heavily sclerotised. It bears three setae, two being below the base of the maxilla lobe and the other near the apex. The lobe itself has one seta. The postmentum is lightly sclerotised and bears two setae anteriorly.

The labrum is a bilobed structure having twelve setae on its dorsal surface arranged in two lines: six setae are close to the edge of the labrum and six larger setae form a line across it. The four large setae below the labrum in fig. 7 (Plate I) are on the clypeus. The ventral surface of the labrum has eight tooth-shaped structures lying on the surface of the upper lip and directed medially (fig. 6, Plate I).

The body setae of the larvae do not vary as far as could be observed throughout the life-history. Figs. 9-12 (Plate II) were taken from third instar larvae. Segments 1-8 of the abdomen are alike except where the prolegs are present on segments 3-6. The small seta *sigma* in fig. 11 (Plate II) anterior to the proleg is

absent in segments 1 and 2. The spiracle of segment 8 is much larger than the other abdominal spiracles. Segment 9 appears to have a rather different arrangement of setae. Both *kappa* and *sigma* setae are absent and *pi* is present. The latter seta is otherwise absent on the abdominal segments. The setal arrangement on the anal plate and associated sclerotised areas (see fig. 12, Plate II) has not been named according to Fracker's convention. The setae on the prothoracic segment are shown in fig. 10. The circle represents the leg. Both *kappa* and *pi* groups are represented by more than one seta. The setal arrangement of the legs is figured in fig. 14 (Plate III). Fig. 13 (Plate III) is a lateral view of a third stage larva. It shows the characteristic forward position of the legs necessitated by the presence of the larval case.

The internal structure of the larva is quite normal. The mandibular glands are long and leaf-like. They are situated dorsal to the proventriculus and are always crossed. The labial glands or silk-glands are elongated and bent strongly back. There are two ovate accessory glands on the silk duct near to where the two ducts join before entering the spinneret.

The oesophagus is long and opens into a thin-walled proventriculus, which almost invariably has a ball of *Pleurococcus* inside it, which gives it a bright green colour. The mid-gut is long, cylindrical and grey in colour. The hind-gut is quite short. It has a thick network of tracheal tubes over the posterior part of its surface. There are three Malpighian tubules on each side of the gut.

The tracheal system is not unusual (fig. 16, Plate IV). The chief point of interest is the tracheal network on the hind-gut. There are two lateral main tracheae connecting the spiracles. Anterior to the prothoracic spiracle they bifurcate. The inner branch supplies the first thoracic, suboesophageal, and the supra-oesophageal ganglia, with a large branch to the mouth-parts and antenna. The upper branch supplies the musculature of the head and prothorax. In the mesothorax a large branch of the main trachae on each side goes to the proventriculus. Besides this there are branches to the ganglia and muscles of the body-wall. The first two abdominal segments have normal ring-like tracheal system with no large branches to the gut. Segments 3 and 8 have a very large branch on each side direct from the spiracle to the mid-gut. There is a very large trachea from spiracle 8 to the net-work on the hind-gut.

The legs are supplied by two branches in each segment. There is a trachea from the dorsal branch from the main trachea, which continues well down the leg anteriorly. Four branches from the ventral trachea supply the posterior and proximal portions of the legs.

The tracheal system in each segment does not form a complete ring. The ventral trachea is complete and connects the two main lateral tracheae. The dorsal trachea is incomplete and does not join its fellow from the other side.

The nervous system presents no unusual features (see fig. 17, Plate IV). There are seven abdominal ganglia. The ventral sympathetic nervous system is figured. The supra-oesophageal and sub-oesophageal ganglia are very large, and pink in colour.

(4) *PUPAE.*

The male pupa of *L. lapidella* (figs. 19-21, Plate V) is about 3 mm. long and 1 mm. wide. The wings are large and are carried laterally, reaching the end of the 6th abdominal segment. The prothorax is very small but both the meso- and metathorax are large. There is a distinct waist due to the narrow first abdominal segment. The abdomen is broadest at the third segment. The antennae and legs are long. The eyes are large and easily noticed. The maxillary palps are represented by two blunt processes immediately below the eyes. Between these is a bilobed structure which is probably the labium. The clypeus and labrum form another biobed sclerite between the eyes.

The setae are similar to those on the larvae. The head, however, shows only two sets, one near the base of each antenna and the other between the eyes.

The pupae of the females of the two species of *Luffia* (figs. 22-27, Plate VI) do not show much difference apart from that of size. The female pupa of the bisexual form is usually about 5 mm. long, while that of the parthenogenetic form rarely exceeds 3·75 mm. in length.

The wings of *L. lapidella* female pupa are relatively slightly smaller than those of *L. ferchaultella*. The maxillary palp of *L. lapidella* is subquadrate and toothed distally (fig. 28, Plate VI), while that of *L. ferchaultella* is rectangular and without the distal tooth (fig. 29, Plate VI). The labrum of *L. lapidella* is more acutely angled distally than is that of *L. ferchaultella*. The labial palp of *L. ferchaultella* is bilobed, while that of the other species is not.

The setae on the head are confined to the base of the antenna, the lateral corners of the anterior-clypeus, and the antero-lateral angles of the frontoclypeus.

(5) *ADULTS.*

(*a*) *Male.* The genitalia of *Luffia* have been described and rather inadequately figured in Pierce and Metcalfe, 1935. These authors consider that the long saccus of this genus and *Bacotia* separates them from the remainder of the Psychids. They say there is nothing in the male genitalia to warrant two genera in the Luffiidae. The genitalia of *L. lapidella* is described by them

as having the sacculus narrow, pointed, with indications of small teeth. Aedeagus stout. Anellus finely pointed. Saccus long, narrow. The anellus is shown in fig. 30 (Plate VII) of this paper as a not very pointed structure bearing small setae on either side of the aedeagus. The sacculus is the pointed structure forming the ventral portion of the harpes (figs. 30 and 31, Plate VII).

The mouth-parts of the male are considerably reduced. Two-segmented labial palps are present. The process on each side of the labium may be the reduced maxillary palps (fig. 32, Plate VII).

The wings are figured in 33 and 34 (Plate VII). The veins are interpreted according to Bradley's notation.

(*b*) *Female*. The females of the two species are compared elsewhere in this paper, pp. 202-206. The characters in which they differ show considerable variation, especially in the parthenogenetic form.

The tentorium of the female is similar to that of the larva, though somewhat stouter (fig. 43, Plate IX). The mouth-parts are reduced ; the labial palps are represented by a bilobed process bearing two setae. The maxillae are probably represented by two projections near the lateral angles of the labrum. The mandibles are absent (figs. 43 and 44, Plate IX). The antennae of the two species are figured (fig. 42, Plate IX). The structure of the ovipositor is shown in the diagrammatic figs. 40 and 41 (Plate IX). Figs. 38 and 39 (Plate IX) show the appearance of the ovipositors in the adult. Figs. 36 and 37 (Plate VIII) indicate the difference in size that exists between the two species.

The internal morphology is normal for a moth. The gut is very reduced. The reproductive system is well-developed and is of the normal Psychid type, having a short tube connecting the bursa copulatrix with the oviduct. The receptaculum seminis and the bursa copulatrix are present but unexpanded. In this respect *L. ferchaultella* appears to resemble *Solenobia lichenella*, described by von Siebold (1857).

The nervous system is well-developed, especially in the head and abdomen. The thoracic ganglia are relatively small.

The separation of the two 'species' of *Luffia*.

(1) *INTRODUCTION*.

The species of Luffiidae recognised by Tutt are not accepted by other authorities. There are three opinions held regarding the relationships between the parthenogenetic and bisexual types.

The latter can be regarded as the original species which is continually producing temporary colonies of parthenogenetic females, while itself remaining undiminished in numbers and vigour.

An alternative possibility is that the bisexual form is producing more permanent parthenogenetic colonies at the expense

of its own type, which is destined to become extinct, leaving a series of parthenogenetic colonies.

A third possibility is that the parthenogenetic race was produced as a result of one or a single series of mutations, and has coexisted ever since with its parent stock.

Meyrick (1928) considers that a race which is merely a parthenogenetic one of a bisexual species has no claim to rank as a species. In his 'British Lepidoptera' he refers to *L. ferchaultella* as a race of the bisexual *L. lapidella*. Meyrick states 'that an essential element of a species is the sexual cross-breeding which counteracts individualism and checks the divergence of units, and by hypothesis this is permanently absent' in such forms as *L. ferchaultella*. He compares the various colonies of the parthenogenetic form to buds, which, like a cutting from a plant, develop in the form of their parents: 'In such circumstances gradual degeneration takes place by exhaustion, and perhaps in the course of 50-100 years the race would gradually become enfeebled and disappear; but as the original stock persists there is no reason why it should not continue to throw off similar decadent races and it probably does so.'

Meyrick's views on the identity of parthenogenetic and bisexual forms are upheld by the opinion of F. M. Jones (1927), who considers that those species of the Psychids which have apparently identical females in both forms are to be regarded as one species (at least, he says, in the genus *Solenobia*).

The work of Seiler (1929) indicates that he thinks the second possibility to be likely. The material he used was *S. triquetrella,* which has a parthenogenetic race structurally indistinguishable from the bisexual form. He says that he has always obtained as a result of his crosses between males of certain bisexual types with females of the corresponding parthenogenetic one, a percentage of intersexes of varying degree of intersexuality. In the crosses out of 315 F_1 larvae, 47 were male, 102 female, and 166 were intersexes. The females were stated to be triploid. The intersexes had reproductive organs which Seiler calls 'Keimdrüsen,' and very complicated genital passages. In some intersexes the hermaphrodite gonad was nearly all ovary, but with a few groups of sperm-forming cells in one or more of the ovisacs. In others, testes with ovocysts were obtained. Seiler (1920) shows that in some localities the parthenogenetic females are the common form, while in other places the bisexual form is found. He considers that the bisexual form is being slowly eliminated.

Tutt undoubtedly believed in the third process, *i.e.* he thought that a parthenogenetic type had been produced on one or a few occasions in the past and had survived as a separate 'species' ever since. His arrangement of the species clearly shows that this was his view.

The factors used to differentiate between two species are:

(*a*) Inability to cross successfully, and produce fertile progeny.

(*b*) The presence of structural differences in one or more stages of the life-history.

(*c*) The presence of differences in the behaviour of the two forms.

In the formation of parthenogenetic colonies from a bisexual species in the manner suggested by Meyrick, structural differences between the colonies and the parent stock would not be expected to be large, since each colony is temporary, and they are being produced from a presumably stable bisexual species. There should be a continuous series of forms connecting the parent type to the most extreme and 'degenerate' type. The amount of variation found between these two extremes will depend on the length of time the colonies can exist and on the variability of the species. In species where there is a slow rate of migration, such temporary parthenogenetic colonies as Meyrick suggests, lasting for less than a hundred years, could not spread very far beyond the range of the parent stock. If this type of race-formation occurs in a slowly migrating species, the parthenogenetic colonies should not extend much beyond the range of the parent species. If the rate of migration is not slow this may not be true; under those conditions the extent to which the parthenogenetic form can spread will depend on its adaptability to different habitats.

Where the parent stock is being eliminated, structural differences should not be large, since the bisexual species is still producing and being replaced by the parthenogenetic form, and the latter would tend to resemble the parent, at least when it first becomes parthenogenetic. Seiler's hypothesis does not take into account any variation which may occur in the parthenogenetic type. As this may well produce quite large differences, the whole group of colonies would show a continuous series of forms from the bisexual type to the indistinguishable, newly-formed parthenogenetic type, and on to the most extreme types of the latter form. It is probably better at present to restrict Seiler's theory to those forms in which the parthenogenetic type does not exhibit any variation in structure from the parent form. Where the parthenogenetic type is so similar to the bisexual species the geographical range of the two forms would be expected to be the same, since an ability in the second form to survive over a different range from that of the bisexual form is not likely in a type so close to its parent.

Vandel (1928) has studied the occurrence of parthenogenetic races of the bisexual *Trichoniscus* (Crustacea, Isopoda). There

are a great number of varieties and local races having somewhat restricted ranges. The females are more numerous than the males. The sex-ratio varies, apparently geographically, though there is no direct relation between the proportion of the sexes and the latitude (and hence the climate). In the south the species contains two distinct races, the bisexual and the parthenogenetic. The change to the parthenogenetic type in the north is not due to the disappearance of the males but to a substitution of one race entirely by the parthenogenetic one. The occurrence of a few spanandrous males in the northern regions may therefore be due to the normal reproduction of a few bisexual females still present and not necessarily through accidental results of parthenogenetic reproduction. The parthenogenetic races are triploid (twenty-four chromosomes) and the bisexual form diploid (sixteen chromosomes) (*cf.* Seiler's crosses with *S. triquetrella*). The parthenogenetic females of *Trichoniscus* are larger than the bisexual form, due to hypertrophy of the cells rather than an increase in the number of cells. Actually the numbers of cells appear to be less in the parthenogenetic form ; if the cells did not hypertrophy they would, therefore, be smaller than the bisexual form. The parthenogenetic females have unused spermathecae (cf. *L. ferchaultella*). Vandel considers that this proves that the parthenogenetic form has come from the bisexual form recently, *i.e.* that the two forms are living together over part of their range, a state of affairs holding for *Luffia* in its continental range. It will be noted that *Trichoniscus* appears to follow Bergmann's Law, that there is a tendency for the larger species of a genus to be present in the north, or rather that northern species tend to be the largest. *Luffia* does not do so.

As far as can be found up to now there is no production of a few males in the parthenogenetic areas of *Luffia* (explained by Vandel as the offspring of ' strayed ' bisexual females). The only evidence of bisexual behaviour in the parthenogenetic *L. ferchaultella* has been the very occasional production of ' calling ' females (see note, p. 206). The distribution of these in England can be only roughly estimated on the records obtained during this work. They appear to be somewhat more common in the southern parts of the species' range.

There appear to be sufficient resemblances between the parthenogenetic forms of *Trichoniscus* and *Luffia* to warrant some further work in this direction.

If the parthenogenetic form was produced from its parent at one operation and has coexisted since, it might be expected to show considerable structural differences from its parent, especially if it has existed long enough to spread over a large range not occupied by its parent. This will be true whether the species is capable of rapid migration or not.

Ability to breed with the male of the parent stock would be more likely to be possible in forms only recently produced, *i.e.* in the first and second types of formation. In these two, the parthenogenetic and bisexual forms have had less time to diverge than they have had in the third type of production.

The three methods of production of the parthenogenetic types can be summarised by noting the characters of any species which had evolved in any one of these ways.

Meyrick Type.

(1) There *must* be continuous variation in structure from the bisexual form to the most extreme parthenogenetic type.

(2) There may be a difference in the geographical ranges of the two types, which will depend on the speed of migration of the species and on the adaptability of the parthenogenetic form.

(3) The parthenogenetic females are quite likely able to breed with the males of the parent stock.

Seiler Type.

(1) There will be no difference in structure between the two forms.

(2) There will probably be no difference in the range of the two forms.

(3) The parthenogenetic females are quite likely able to breed with the males of the parent stock.

Tutt Type.

(1) The variation in structure between the two forms will be almost certainly discontinuous.

(2) It is probable that the geographical ranges of the two forms will differ.

(3) The parthenogenetic females may not be able to mate with the parent stock males.

As regards these three criteria, the structural differences between the females are discussed on p. 202 et seq. It is shown that *L. lapidella* is on the average larger and has 14-segmented antenna. *L. ferchaultella* is smaller, and this results in a reduction in various organs (*e.g.* antennae, tarsi, etc.), and the antennae very rarely have more than twelve segments. In geographical range (see p. 206) (at least in England and the Channel Isles) the forms differ markedly. It is shown on p. 207 that males of *L. lapidella* do not appear to mate with the females of *L. ferchaultella*. Tutt's views as to these forms seem, therefore, to be nearest the truth.

(2) Comparison of structure and habits of *L. lapidella* and *L. ferchaultella* females.

The two forms of *Luffia* occur together in the Channel Isles. A collection of larvae and pupae from walls in Guernsey were mostly *L. lapidella*. There were four specimens of *L. ferchaultella* females in a total of thirty-one females bred from the Guernsey material [based on structural sizes and characters of *L. ferchaultella* from English material].

A collection of larvae from trees in Jersey produced one individual with fourteen segments in the antenna and one with thirteen. All the others were 12-segmented. All the other characters in the adults in this series were within the *L. ferchaultella* range.

The only differences observed in the structure of the two types were the 14-segmented antenna of the bisexual form and the 12-segmented antenna of the parthenogenetic form. The body size of the latter was distinctly smaller, but this was difficult to measure.

The following table compares the average sizes of certain structural characters of the adult females from the Channel Isles. Twenty-seven specimens of *L. lapidella* were obtained from Guernsey. Their average size is tabulated. Thirteen specimens of *L. ferchaultella* from Jersey and Guernsey were measured.

In the following tables the terms used are as under:—

Head = head diameter of adult female;

Ant. = number of segments on the antenna;

T.N. = Tarsal Number: the number of tarsal joints on all six legs;

A, B, C, D, are the lengths of three ovipositor rods. Strut of segment 8 is rod A. The strut of segment 9 is rod B. The accessory strut of segment 9 is rod C; the length of the two arms of this strut were measured as rod D (see figs. 40 and 41, Plate IX);

Wing-ratio = length/breadth of the fore-wing.

In addition to the actual sizes of the structures studied, a number of ratios were obtained both for localities and for individuals. The ratios used were from ovipositor rod lengths, head diameters, tarsal numbers and antennal numbers. In these ratios it was more convenient to use the head diameter expressed as micrometer divisions than as actual sizes in millimetres.

TABLE I.

COMPARISON OF CHARACTER-SIZES.

	Head mm.	Ant. segments.	T.N.	A mm.	B mm.	C mm.	D mm.	Wing-ratio.
L. lapidella ...	0.432	14.0	24.0	1.44	3.69	1.23	0.82	5.23
S.D. (27) ...	0.035	0.0	0.0	0.18	0.39	0.15	0.11	2.90
L. ferchaultella	0.384	12.0	23.77	1.28	3.27	1.14	0.78	2.94
S.D. (13) ...	0.020	0.0	0.58	0.15	0.22	0.09	0.05	1.09

In the above and all following tables S.D. (Standard Deviation) is given from $S^2 = \frac{\Sigma (\bar{x} - x)^2}{n - 1}$, *i.e.* the standard deviation of the population. The number in brackets after S.D. refers to the number of specimens in the sample used.

All the differences between the two species given in this table are mathematically significant except between C and D, which were just inside the limits set.

TABLE II.

COMPARISON OF RATIOS.

	B/A	A/C	Head/Ant.	Head/T.N.	Ant./T.N.
L. lapidella ...	2.57	1.19	1.82	1.06	0.58
L. ferchaultella ...	2.54	1.12	1.87	0.94	0.51

The range of variation of the characters were slightly different in the two species, but the limits of both overlapped. The figures for the females of the parthenogenetic species obtained from the Channel Isles are tabulated below between those for the *L. lapidella* from Guernsey and those for *L. ferchaultella* from England. The latter are based on measurements of more than 500 specimens. The chief point to be noted is that the antenna always had twelve segments in the Channel Isles parthenogenetic forms, and that the tarsi were almost always 4-segmented. They also tended to be nearer *L. lapidella* in structure. This is enlarged upon below.

TABLE III.

RANGE OF VARIATION IN CHARACTER-SIZE.

	L. lapidella (Guernsey).	*L. ferchaultella* (Jersey).	*L. ferchaultella* (England).
Head diameter	0.35-0.49 mm.	0.35-0.41 mm.	0.29-0.42 mm.
Antennal segt.	14	12	usually 12 or less
T. number ...	24	22-24	12-24
Ovip. rod A ...	1.04-1.78 mm.	0.96-1.48 mm.	0.59-1.55 mm.
Ovip. rod B ...	3.11-4.81 mm.	2.81-3.48 mm.	1.78-3.85 mm.
Ovip. rod C ...	1.04-1.55 mm.	1.04-1.33 mm.	0.44-1.41 mm.
Ovip. rod D ...	0.66-1.04 mm.	0.66-0.88 mm.	0.37-0.95 mm.
Wing-ratio ...	1.0-16.0	1.0-5.7	0.3-7.0

There are indications that the species *L. lapidella* in the Channel Isles may exhibit bimodal variation with a small form coexisting with a larger one. The specimens of *L. ferchaultella* obtained from Jersey appear to resemble the small types in the collection of adults from Guernsey, which are presumably *L. lapidella*. These smaller *L. lapidella* have fourteen segments to their antennae. Apart from this character they are almost identical with the 12-segmented antennae types from Jersey, which were certainly *L. ferchaultella*. Unfortunately there was not sufficient material available to investigate this more fully. There were barely enough adults to show the bimodal character at all. Further investigation of the species in the Channel Isles appears to offer several interesting problems. There were two specimens in the Jersey collection of females, which were *L. lapidella*. They possessed 14-segmented antennae and they appeared to belong to the large type of *L. lapidella*. There were also four specimens of individuals with 12-segmented antennae in the Guernsey collection which were certainly *L. ferchaultella*.

The adults bred from material collected in England have included a few similar to the two irregular females from Jersey.

Three specimens with 14-segmented antennae were obtained from larvae collected near Wallingford (Berks). The head diameter was large but within the *ferchaultella* range, the tarsi were 4-segmented, but otherwise these specimens were quite normal large *L. ferchaultella*.

A single similar specimen was bred from Steyning, near Brighton. This had a tarsal formula of 3-4-4 and was, except for the antenna number, a normal type of *L. ferchaultella*.

Another single female with 14-segmented antennae was bred from larvae feeding on lichens on Stonehenge monoliths. There was also one specimen from these larvae with thirteen segments in the antenna. The former individual was a very large *L. ferchaultella* which could structurally be regarded as a small *L. lapidella*. The specimen with 13-segmented antennae is intermediate between the normal *ferchaultella* and the '*lapidella*' specimen (see Section 3 below for consideration of Tutt's belief in the occurrence of *L. lapidella* on rock-lichens).

TABLE IV.

STONEHENGE 'LAPIDELLA' TYPES.

	Head mm.	Ant. segments.	T.N.	A mm.	B mm.	C mm.	D mm.	Wing-ratio.
Average *ferchaultella* for locality	0.371	11.80	22.50	1.12	2.94	1.01	—	2.37
S.D. (50) ...	0.024	0.79	1.82	0.13	0.32	0.12	—	0.71
Female (13 ant. segs.)	0.391	13.00	24.00	1.41	3.26	1.18	0.74	2.00
Female (14 ant. segs.)	0.425	14.00	24.00	1.33	3.55	1.18	—	4.00

Similar individuals with 13-segmented antennae have been bred from Horsham and Petworth (Sussex) and from Oxshott (Surrey). All were large *ferchaultella* types, only one having a tarsal formula 4-4-4.

The occurrence of these types in England where the male of *L. lapidella* has never been bred seems to indicate that the two forms cannot be distinctly separated by structural definitions. The two characters that are apparently the most distinctive are the antenna number, which is always fourteen in *L. lapidella*, but only rarely so in the smaller form, and to a less degree the form of the rudimentary wings. The hind-wing is only rarely present in the English specimens of *L. ferchaultella* and the fore-wing is generally shorter than in the *L. lapidella* females. Whether this holds over the continental range of the genus is doubtful (see also Table I).

There appear to be slight differences in the sclerites in the face of the female pupae of the two species. These are noted in the description of this stage. The bisexual pupa is distinctly larger than that of the parthenogenetic type.

The larvae of the two forms were almost impossible to separate except by their size. The few larvae obtained of the bisexual

species were definitely larger than the biggest larvae collected in England. The abdomens of the larger form were possibly slightly darker grey. The setae on the head capsule were the same as those observed for *L. ferchaultella*.

Probably the two species could be differentiated by a study of the larval instars. The instars have been separated in the English specimens, but sufficient material of the Channel Isles specimens could not be obtained for this to be done with them.

The most distinct difference between the two forms is provided by the behaviour of the animal. The parthenogenetic habit of the smaller form differentiates it clearly from the other type. As a result of this habit the female does not sit on the case after emergence, waiting to mate with the male, but commences to oviposit immediately. Even this characteristic is not absolute, since a few specimens of *L. ferchaultella* have been observed to 'call'* before oviposition. The individuals which have done so have been large specimens of *L. ferchaultella,* so this habit-variation can be compared with the occurrence of '*lapidella*' structural types in colonies of the parthenogenetic form.

In England the larva of *L. ferchaultella* feeds on both tree- and rock-lichens. Apparently in the Channel Isles the rock-lichens may support some *L. ferchaultella*. Whether the converse holds is uncertain; it appears at any rate that *L. lapidella* does not occur as much on tree-lichens as does *L. ferchaultella* on rock-lichens. More collection of larvae in the Channel Isles will be necessary before that point can be cleared up.

(3) Comparison of the Geographical Range of the Species of *Luffia*.

Tutt (1899 and 1900) accepts *L. lapidella* as a British species, and gives four localities, two of which he regarded as uncertain.

The first is from Carnarvonshire, between Conway and Llandudno. Some larval cases reputed to be those of *L. lapidella* from a stone wall near Conway, which are in the Manchester Museum, have been examined. It is not certain that these cases are *Luffia* cases at all. The specimens are empty larval cases, so that identification of them is very uncertain. I think that they probably belong to a species of *Solenobia*. A collection of cases made in the Conway district did not yield any specimens of *Luffia,* though many *Solenobia* were found. Except for this record, and an equally dubious one from Howth, Dublin, the genus is unknown north of a line from Leominster to Cromer.

The other records of *L. lapidella* are from various parts of the Dorset coast and from Stonehenge.

* 'Calling' consists in extending the abdomen in a characteristic way and probably emitting a scent which attracts the male.

Larvae and pupae have been collected from Stonehenge. No males were obtained. The females which emerged, about fifty, were all like normal adults of *L. ferchaultella* in size [except two specimens mentioned above], appearance and habits. Fertile eggs were laid without mating. The fact that the larvae were feeding on rock-lichens was the chief reason why previous authors had called them *L. lapidella*. The absence of males and the parthenogenetic development of the eggs was ignored in identifying these specimens from the Stonehenge monoliths. The feeding habits of the larvae are not an entirely reliable guide to the species.

Similar conditions prevail in the Dorset localities. The reference which Tutt uses when he claims *L. lapidella* as a member of the fauna of Dorset is in Bankes (1896). The larval cases were recorded by Bankes as being those of a *Solenobia* sp. Here again Tutt called these specimens *L. lapidella* because of the larval feeding habits.

Burrows (1923) has spent a considerable time attempting to obtain British specimens of *L. lapidella* males without success. He has not seen any female specimens of this species from the south coast which do not agree in structure with *L. ferchaultella*.

L. lapidella is quite common on the Continent, and in the Channel Isles, where it occurs on the lichen-covered rocks and walls, and also possibly on trees. In England no one has ever found an undoubted example.

During the year 1935-36 no males have been bred from more than 6,000 larvae collected in the course of this study. A small collection of less than a hundred larvae from the Channel Isles produced twenty-six specimens of *L. lapidella* males.

It is therefore fairly certain that the bisexual species is not a member of the British fauna.

The range of the parthenogenetic *L. ferchaultella* in England is described elsewhere [McDonogh, 1939]. It covers an extensive area not occupied by the bisexual form, from the south coast as far west as Torquay and south of a line through Cardiff, Leominster, Warwick and the Wash.

(4) Attempts to pair male *L. lapidella* with female *L. ferchaultella*.

In 1917 Burrows bred a *L. lapidella* male from Guernsey material. When introduced to a female of *L. ferchaultella* this male became violently excited. Copulation appeared to occur, but this lasted half an hour instead of the few minutes that is the rule in the Psychids. The female failed to oviposit and died without doing so. The failure to lay eggs suggests that either the female or the treatment she received was abnormal.

This experiment was repeated by me in 1935 with males from Guernsey. Females of the parthenogenetic 'race' were bred from material collected in various parts of South England. The experiments were as unsuccessful as those of Burrows. The males could not be induced to mate at all with *L. ferchaultella*. A few of the males exhibited signs of excitement when put with a newly-emerged female and obviously tried to copulate, but in every experiment they failed. The females eventually laid eggs, but these were certainly normal unfertilised ones. The same males in a few examples and also some of their brothers successfully mated with *L. lapidella* females bred from the same Guernsey material.

The success of Seiler's crosses with *Solenobia*, where the sexual and parthenogenetic forms are more nearly identical in structure, suggests that the failure in *Luffia* is significant, and that here we are dealing with more distinct forms. It must be noted that though a percentage of the crosses in *Solenobia* produced males, the intersexes and the triploid females were abnormal. Though the two forms were structurally alike, they were not to be regarded as completely conspecific, since their progeny were not normal and were probably infertile.

The forms of *Solenobia* used by Seiler were more closely related to each other than are the two types of *Luffia*, since there are greater structural differences between the forms of the latter genus. If the former should not be regarded as completely conspecific, the two forms of *Luffia* should be considered even less identical on the evidence given by the interbreeding experiments alone.

Summary.

The morphology of the genus *Luffia* is briefly described, the structure being chiefly shown by means of forty-six figures.

The validity of the species recognised by Tutt is discussed and his views are upheld. The views of Meyrick and Seiler are also considered, but they appear unsuited to *Luffia*.

The structure of the females of the two species and the range of the species are compared, and the inability of the two forms to interbreed is described.

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Fig. 1.—Head of larva, dorsal.

Ant: antenna. at: tentorium pits. Clp: clypeus. es: epistomal suture. Fr: frons. Frs: frontal suture. Lm: labrum. Lo: lobe of maxilla.

Fig. 2.—Head of larva, ventral.

AT: anterior arm of the tentorium. C: cardo. Frs: invagination of the frons. HB: hypostomal bridge. HyR: hypostomal region. Prmt: prementum. Ptmt: postmentum. PT: posterior arm of the tentorium. St: stipes. SS: submental sclerites. TB: tentorial bridge. Other lettering as fig. 1.

Fig. 3.—Mandibles.

Fig. 4.—Tentorium, dorsal.

IH: invagination of hypostomal sclerite. Hst: hypostome. IF: invagination of the frons. Other lettering as above.

Fig. 5.—Ocelli and Antenna, lateral.

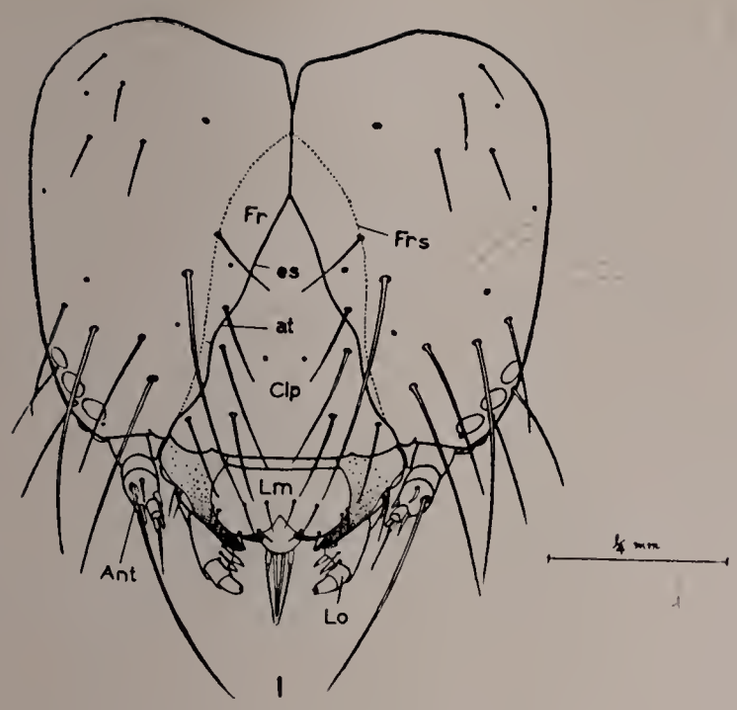
Fig. 6.—Labrum, ventral.

Fig. 7.—Labrum, dorsal.

Fig. 8.—Maxillae and Labium, ventral.

Sr: spinneret. Other letters as before.

PLATE I.



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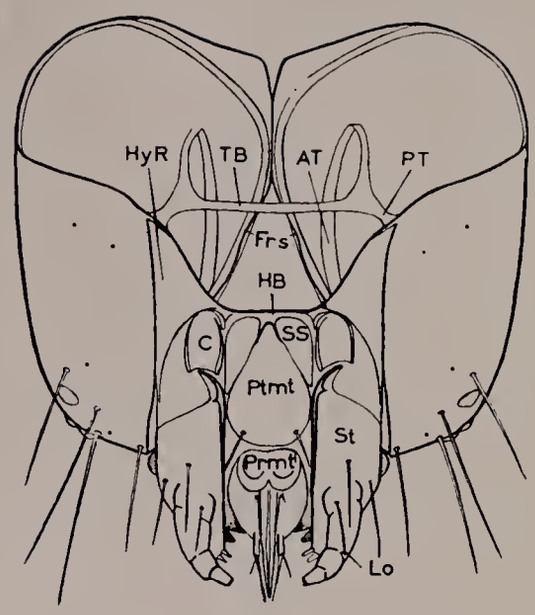

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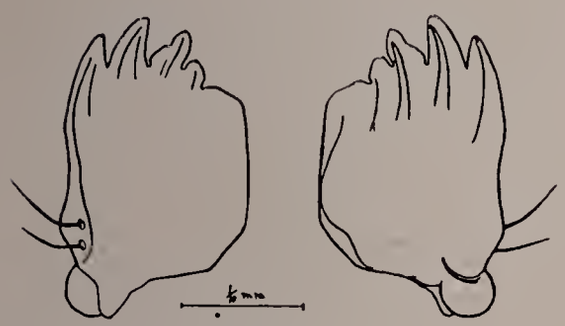

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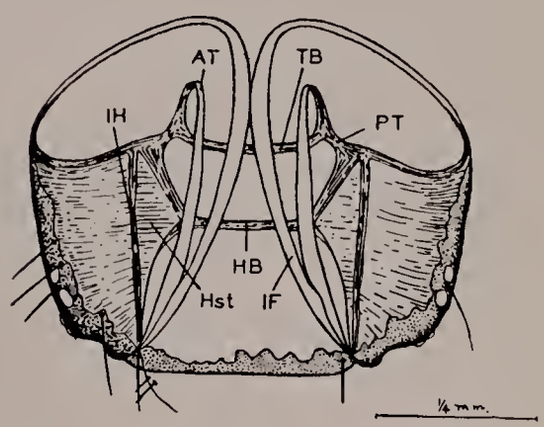

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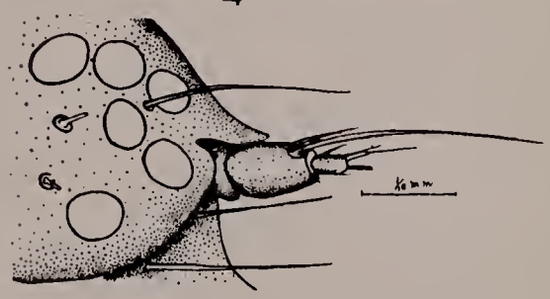

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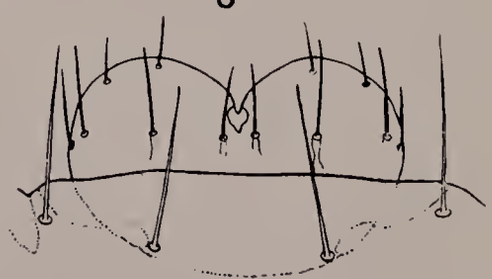

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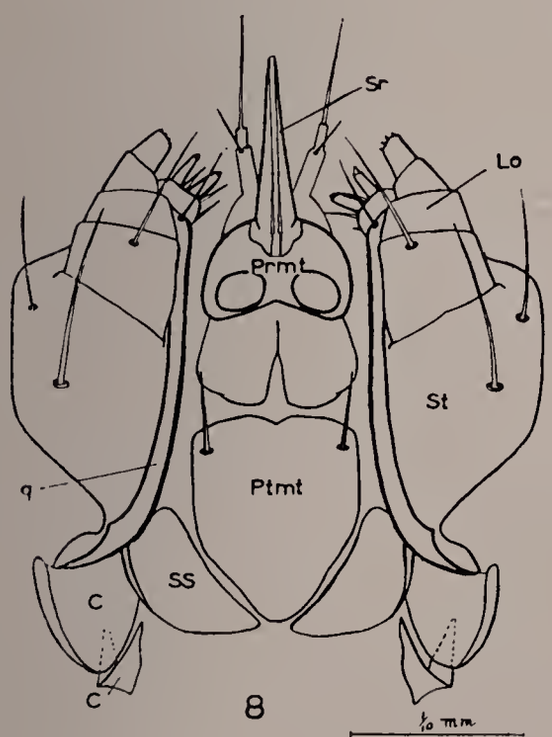

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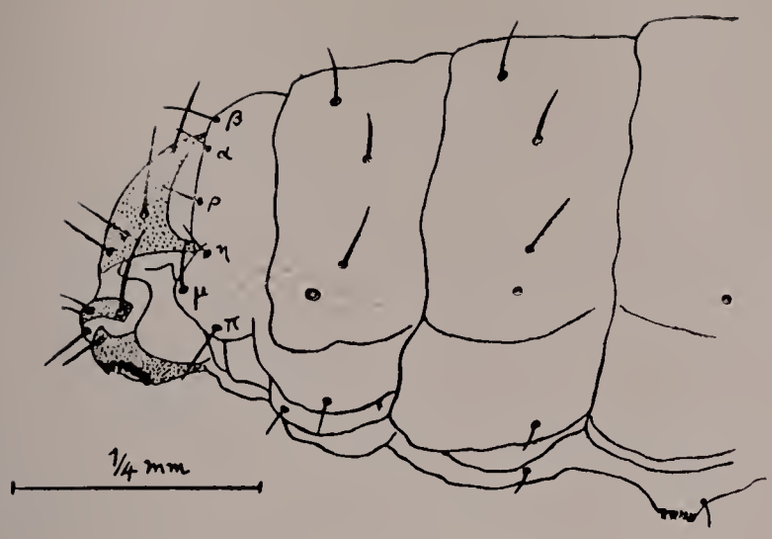

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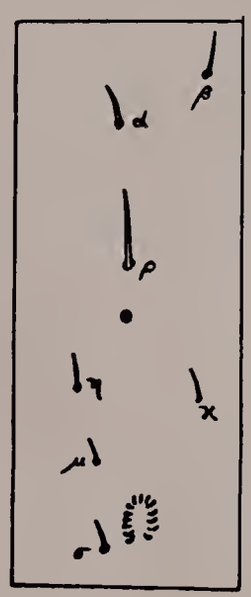

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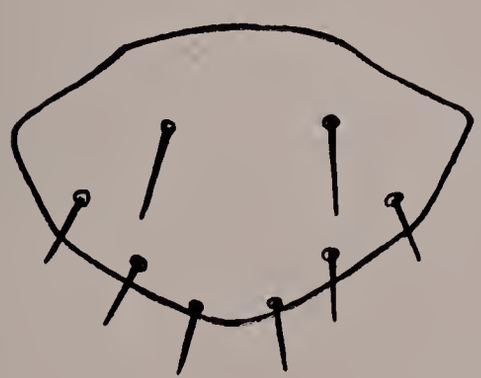

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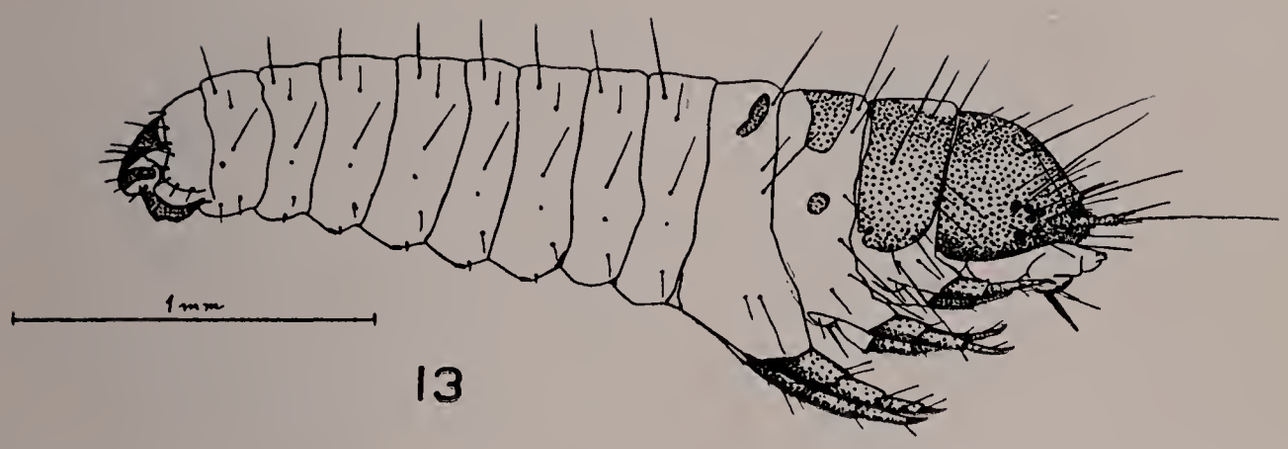
FIG. 9.—Posterior region of abdomen of larva, lateral.
FIG. 10.—Prothoracic setae map, third instar.
FIG. 11.—Third abdominal setae map, third instar.
Figs. 10 and 11 are lettered after Fracker.
FIG. 12.—Anal plate, dorsal.

PLATE III.



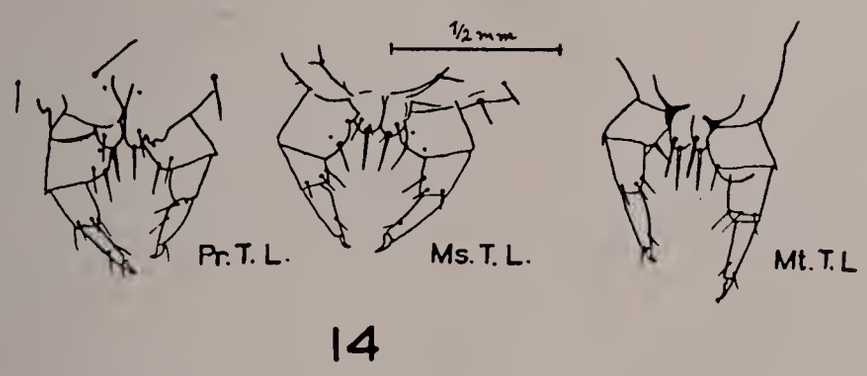


FIG. 13.—Third instar larva.

FIG. 14.—Legs of larva, anterior.
PrL: prothoracic legs. MsL: mesothoracic legs. MtL: metathoracic legs.

Fig. 15.—Alimentary canal of larva

A Gl: accessory gland of the silk-duct. HG: hind-gut. L Gl: labial gland, silk gland. MG: mid-gut. M Gl: mandibular gland, salivary gland. Mph T: malpighian tubules. Prov: proventriculus.

Fig. 16.—Larval nervous system.

MsT G: mesothoracic ganglion. MtT G: metathoracic ganglion. Prt G: prothoracic ganglion. SubO G: suboesophageal ganglion. SuprO G: supraoesophageal ganglion. V Sys: ventral sympathetic system.

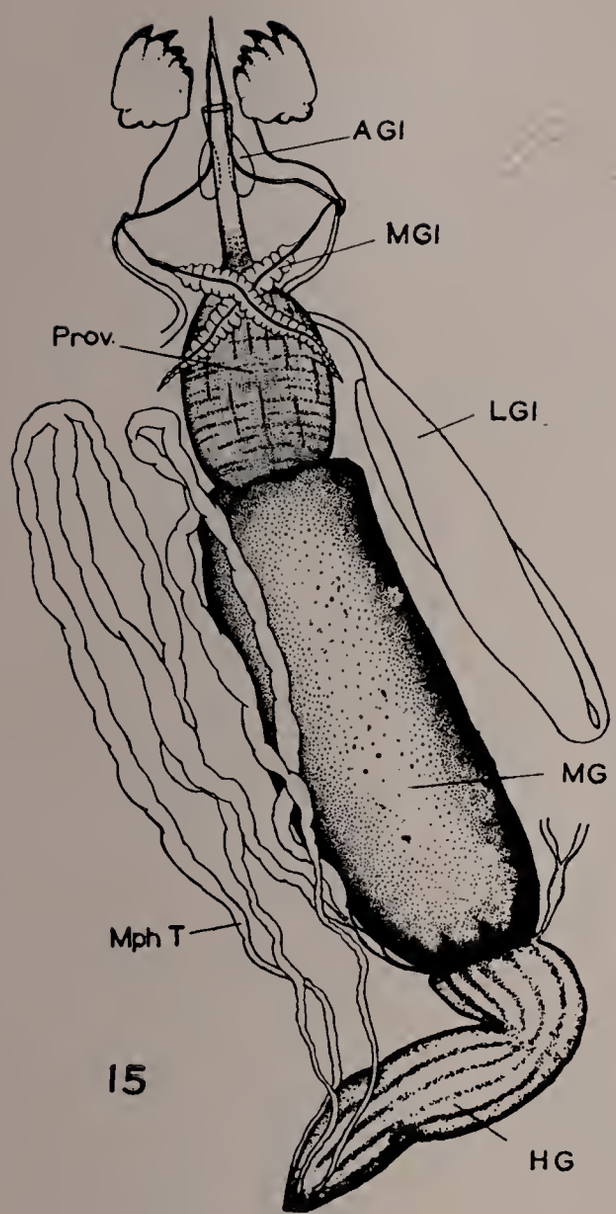
Fig. 17.—Lateral view of head ganglia.

Lettering as before.

Fig. 18.—Tracheal system of larva.

A leg: branch trachea to anterior part of leg of that segment. DT: dorsal trachea. Long T: longitudinal trachea. P leg: branch trachea to posterior part of the leg of that segment. ProT Sp: prothoracic spiracle. to Prov: branch to the proventriculus. Rn: rectal net of trachea. Sp 1 and 2: spiracles of first and second abdominal segments. VT: ventral trachea.

PLATE IV



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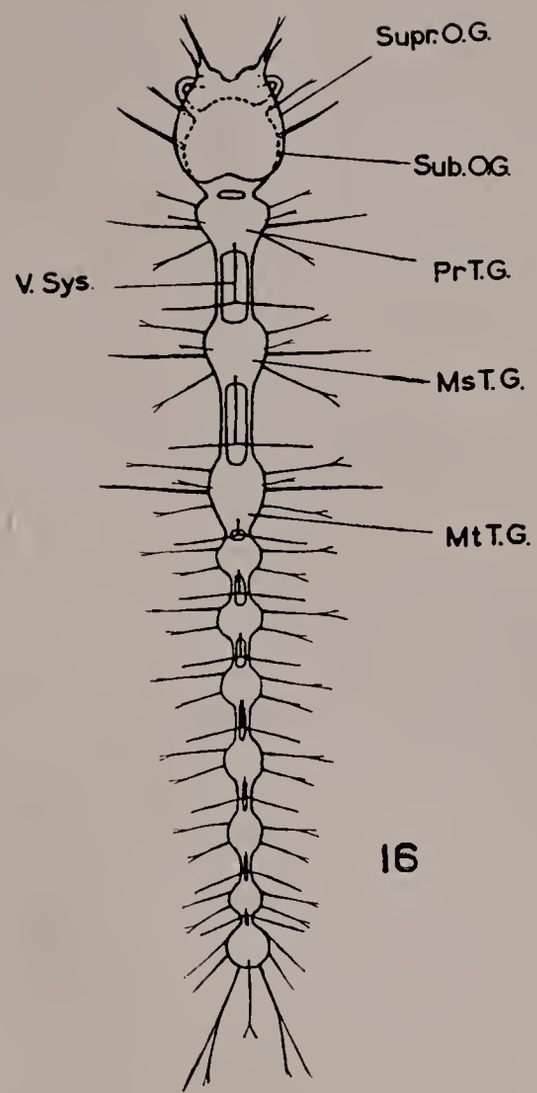

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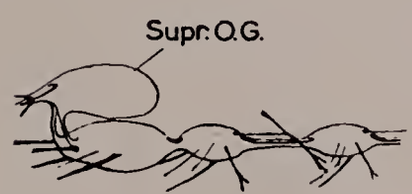

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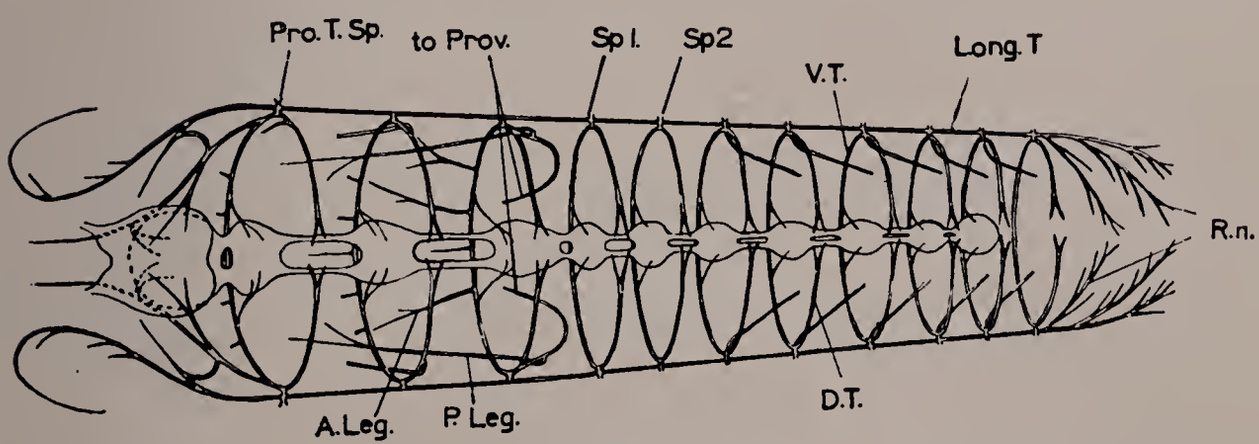

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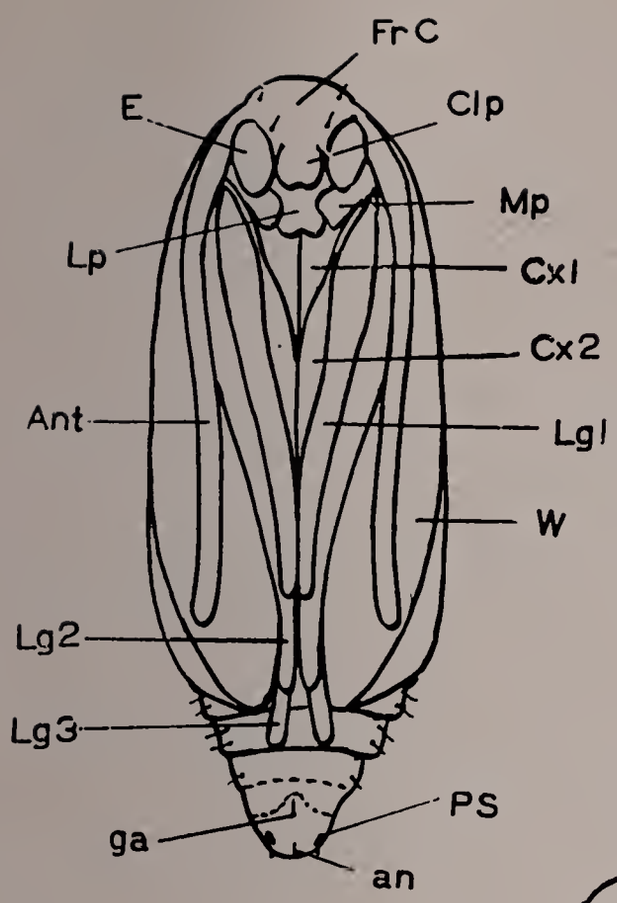

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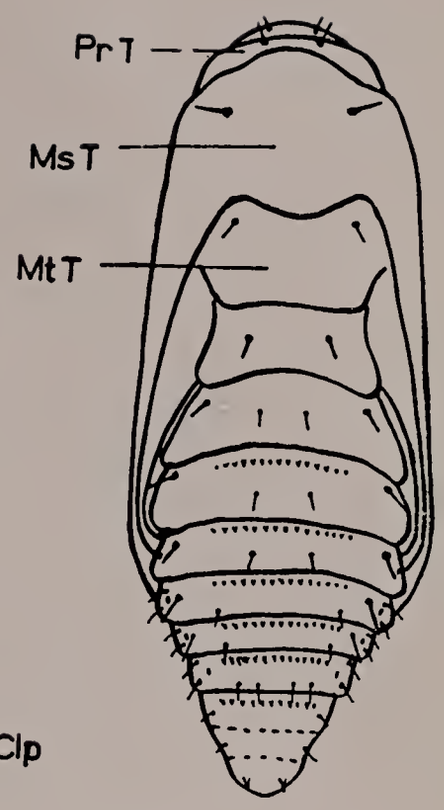

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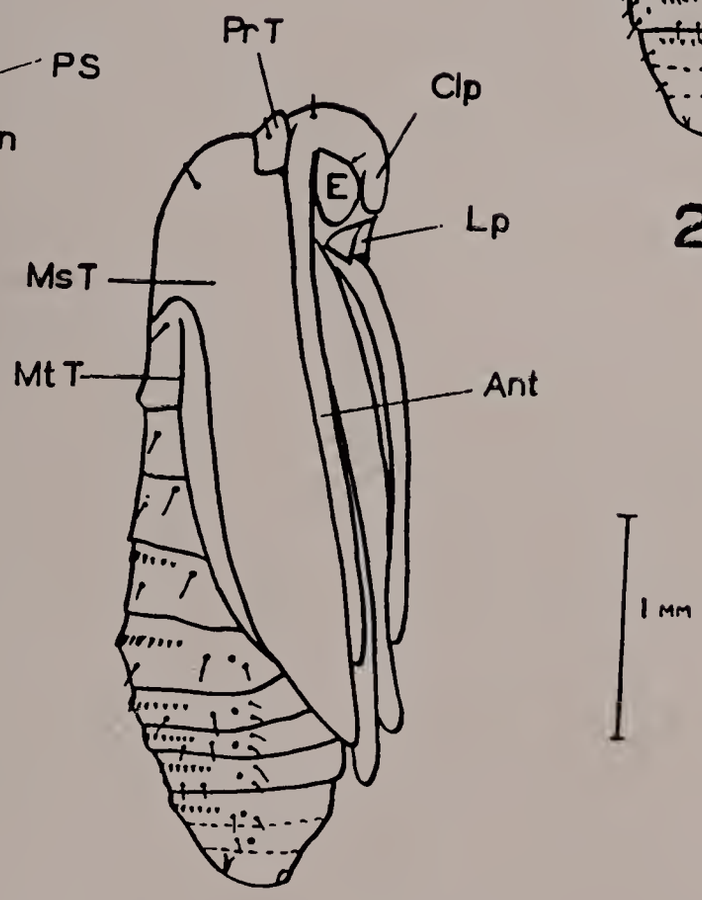

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Fig. 19.—*Luffia lapidella* male pupa, ventral.

Ant: antenna. Clp: clypeus. Cxl-3: coxae of legs. E: eye. FrC: fronto-clypeus. L: labrum. Lp: labial palp. Md: mandible. Lgl-3: legs. Mp: maxillary palp. W: wing. an: anus. ga: genital aperture. Ps: scar of proleg.

Fig. 20.—Dorsal view of male pupa.

MsT: mesothorax. MtT: metathorax. PrT: prothorax.

Fig. 21.—Lateral view of male pupa.

Lettering as fig. 19.

Fig. 22.—Pupa of *Luffia lapidella* female, ventral.
A Clp: anterio-clypeus. Other lettering as in fig. 19.

Fig. 23.—Lateral view of female pupa of *L. lapidella*.
Lettering as in fig. 19.

Fig. 24.—Dorsal view of above.
Lettering as in fig. 20.

Fig. 25.—*Luffia ferchaultella* female pupa, ventral.
Lettering as in fig. 22.

Fig. 26.—Lateral view of pupa of *L. ferchaultella* female.
sp: spiracle. Other lettering as in fig. 19.

Fig. 27.—Dorsal view of above.
Lettering as in fig. 20.

Fig. 28.—Face of the pupa of *L. lapidella* female.
Lettering as in fig. 22.

Fig. 29.—Face of the pupa of *L. ferchaultella* female.

PLATE VI.

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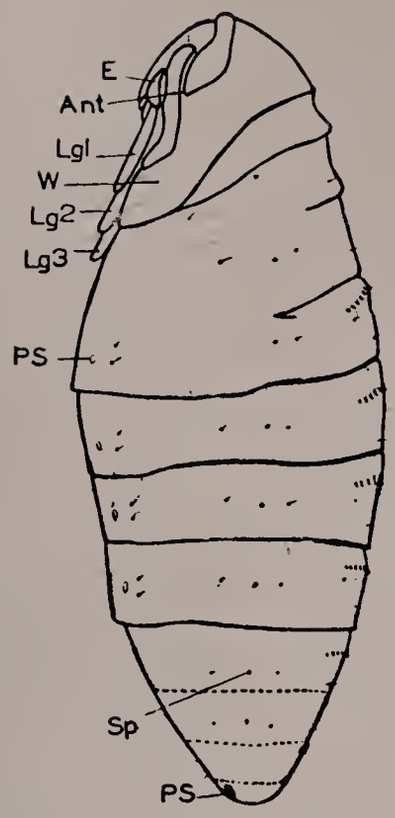

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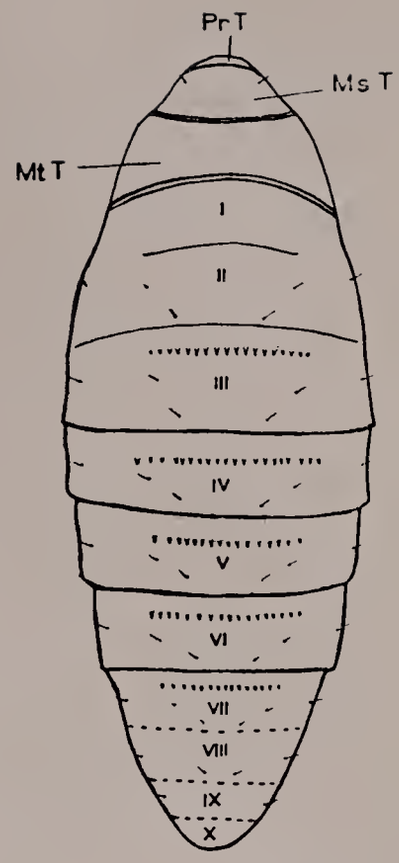

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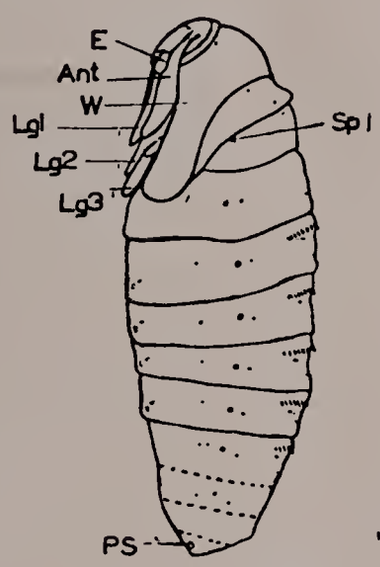

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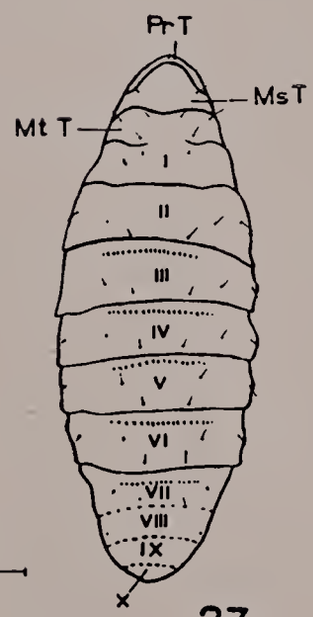

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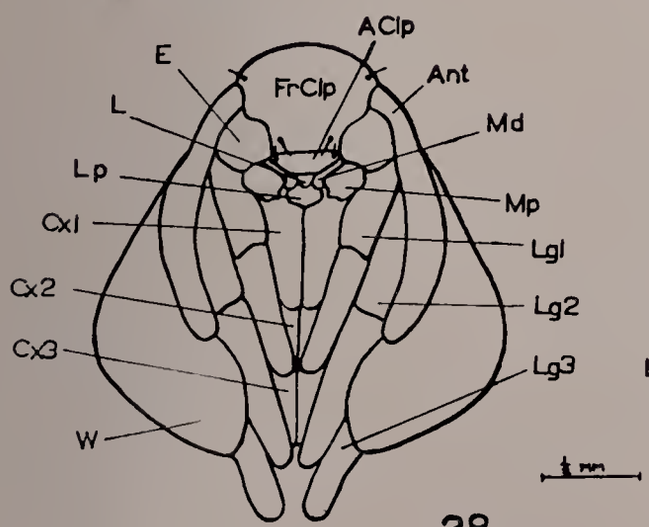

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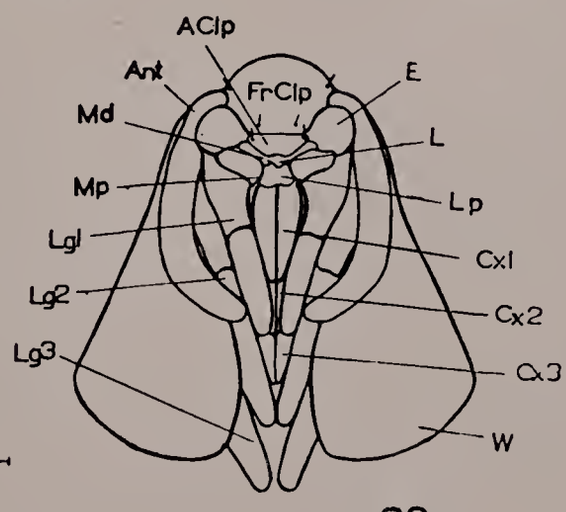

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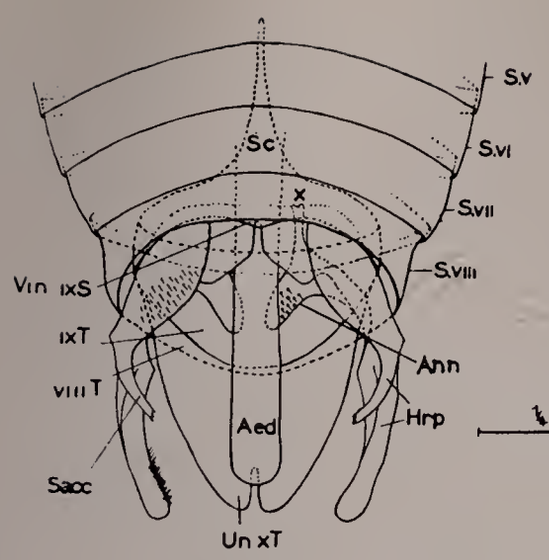
PLATE VII.



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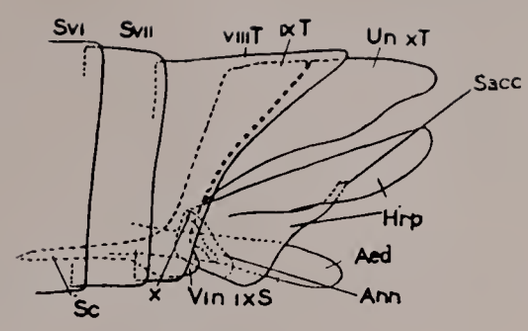

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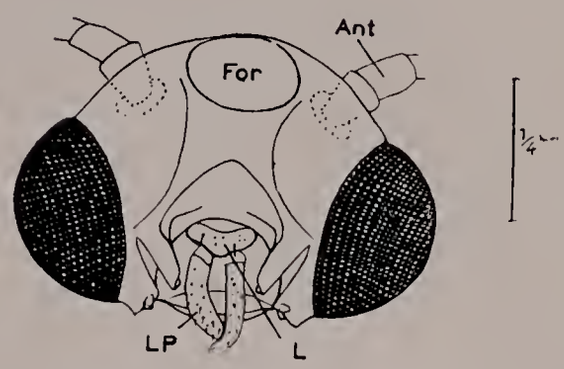

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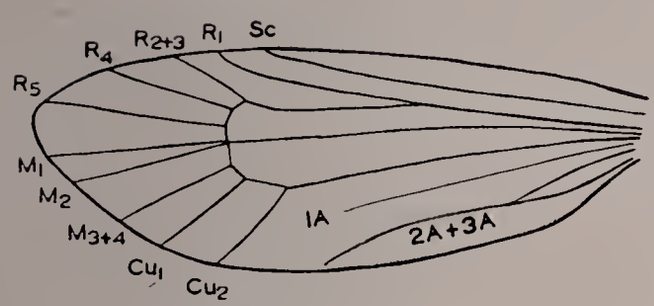

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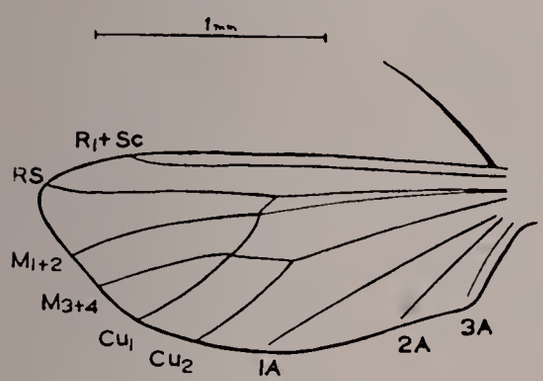

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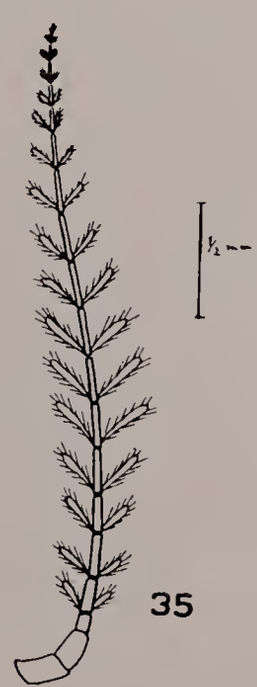

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Fig. 30.—Genitalia of male *Luffia lapidella*, ventral.
Aed: aedeagus. Ann: annellus. Hrp: harpes. Sacc: sacculus. Sc: saccus. Un xT: uncus (tergite of segment X). Vin ixS: vinculum (sternite of segment IX). ixT: tergite of segment IX. x: articulation of the annellus with the ix sternite.

Fig. 31.—Lateral view of male genitalia.
Lettering as in fig. 30.

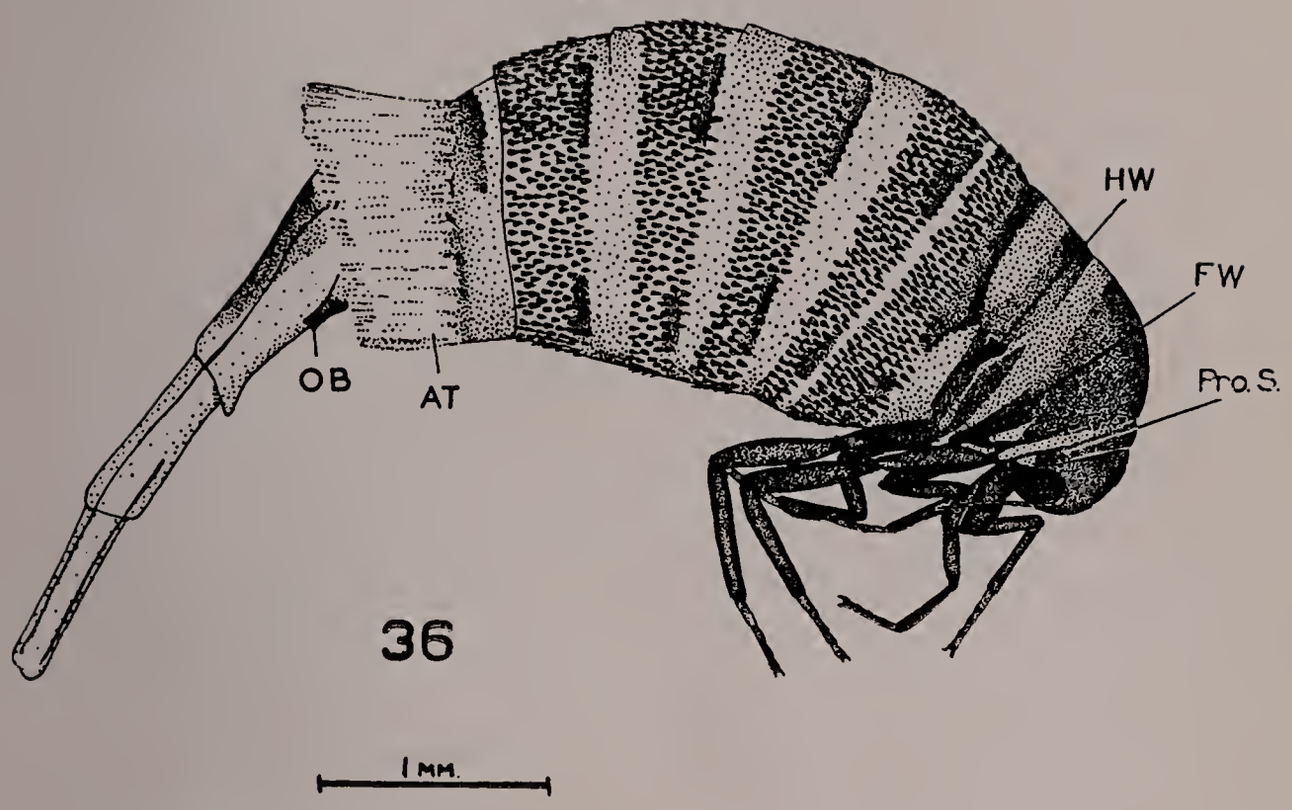
Fig. 32.—Ventral view of the head of the male.
Ant: antenna. L: labium. Lp: labial palp.

Fig. 33.—Forewing of the male.

Fig. 34.—Hindwing.
Wing veins interpreted according to Bradley.

Fig. 35.—Antenna of the male.

PLATE VIII.



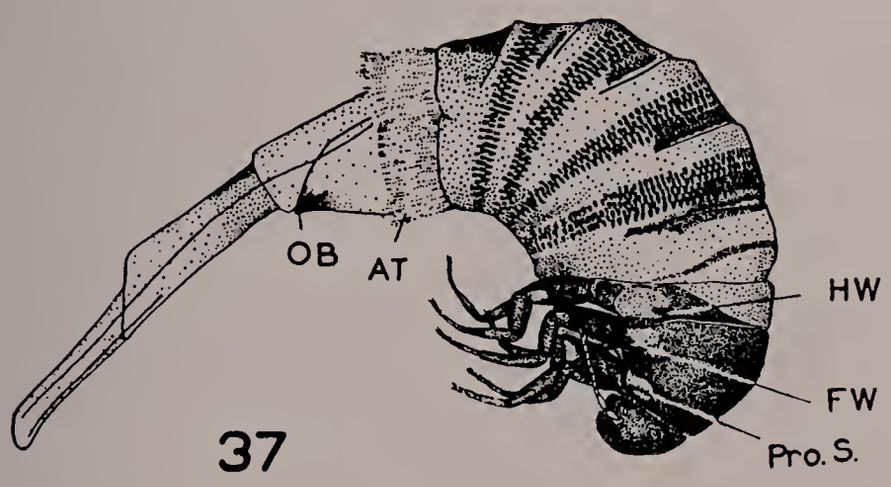


FIG. 36.—*Luffia lapidella* female adult, lateral.
AT: anal tuft. FW: forewing. HW: hindwing. OB: ostium bursa. ProS: prothoracic spiracle.

FIG. 37.—*Luffia ferchaultella* female.
On same scale as fig. 36. Lettering as fig. 36.

Fig. 38.—Ovipositor of *L. lapidella,* approx. ventral.

AcStix: accessory strut of IX. St viii: strut of segment VIII. St ix: strut of segment IX. Other letters as fig. 36.

Fig. 39.—Ovipositor of *L. ferchaultella,* lateral.

Fig. 40.—Diagrammatic ovipositor, extended.

Atm: arthrodial membrane 'segment.' OG: genital opening. Other letters as in fig. 38.

Fig. 41.—Same as above in the contracted state.

Fig. 42.—(A) Antenna of *L. lapidella.*

(B) Antenna of *L. ferchaultella.*

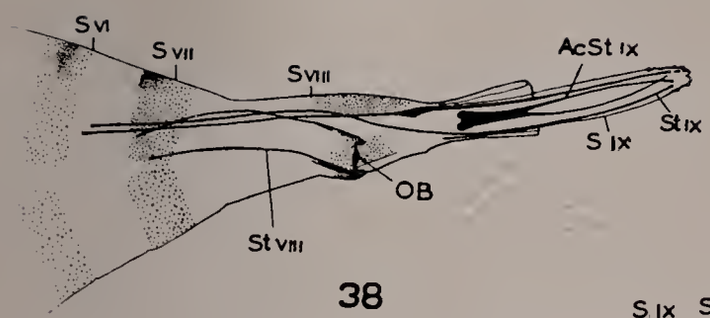
Fig. 43.—Head of *L. ferchaultella,* ventral.

Ant: antenna. AT: anterior arm of tentorium. E: eye. Lm: labium. Lp: labial palp. MxP: maxillary palp. PT: posterior arm of tentorium. TB: tentorial bridge.

Fig. 44.—Head of *L. ferchaultella,* dorsal.

cs: coronal suture. Fr: frons. fs: frontal suture. Other letters as in fig. 43.

PLATE IX.



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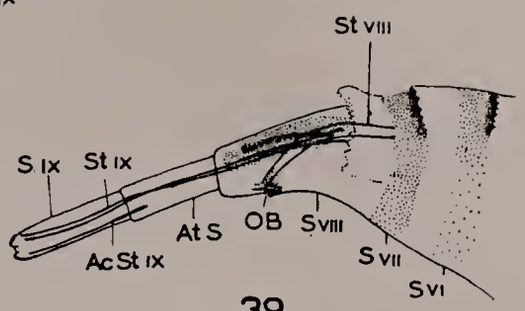

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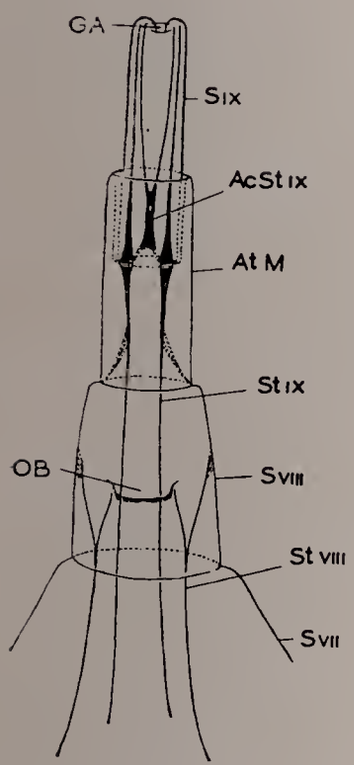

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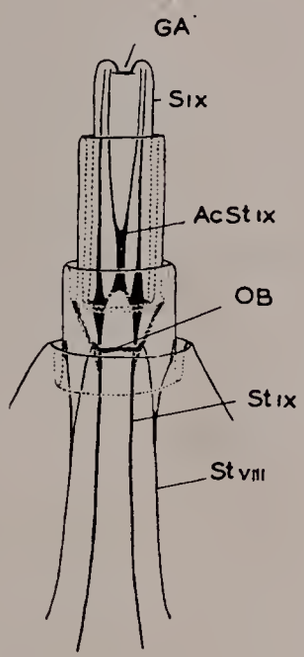

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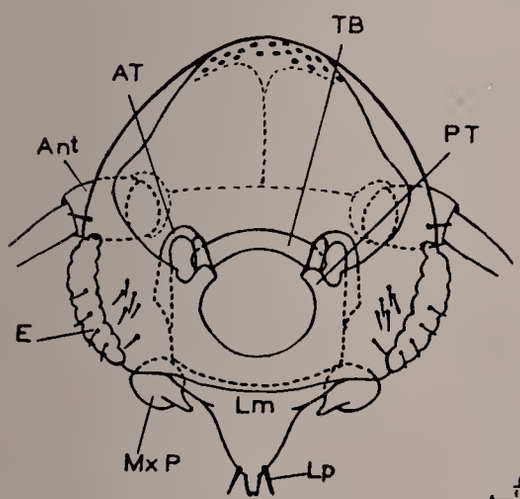

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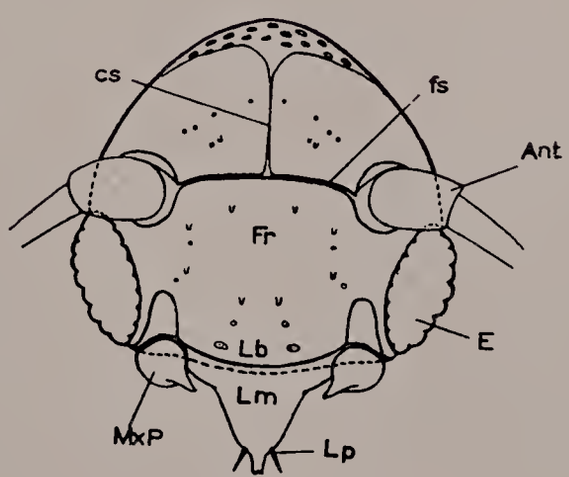

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CONTENTS.

McDonogh, Richard S., B.Sc., D.I.C., The Morphology of *Luffia Ferchaultella* (Stephens) and a comparison with *Luffia Lapidella* (Goeze) (Lep., Psychidae).

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